

How does bromeliad distribution structure the arboreal ant assemblage (Hymenoptera: Formicidae) on a single tree in a Brazilian Atlantic forest agroecosystem?

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Abstract

Some tropical agro-forestry systems contribute to the maintenance of diverse vascular epiphytes. Due to high bromeliad density, they may resemble native Brazilian Atlantic forest canopies offering resources for organisms living at the top of the trees such as ants. The present study investigates the importance of epiphytes on trees planted to shade cocoa plantations as habitats for ants. The following hypotheses were tested: (I) The bromeliad structure and location (distance from the tree centre) in the canopy affect ant species richness; (II) epiphytes with suspended soil support higher ant species richness; (III) the composition of ant assemblages differs between bromeliads with and without suspended soil and also as a function of bromeliad size; (IV) epiphyte-dwelling ant species composition depend on the epiphyte genera and species. The study was carried out in March 2007, in a cocoa agro-forestry area froms the Cocoa Research Center, Ilhéus, state of Bahia, Brazil. On a single *Erythrina* tree, 47 ant species were collected in 36 out of the 52 bromeliad epiphytes sampled. The ant composition was strongly affected by the presence of suspended soils where many bromeliads root. We detected a significant negative correlation between location of the bromeliad and ant richness. The ant species richness and composition depended on the epiphyte size and the occurrence of suspended soil. These results stress the importance for biodiversity conservation in agroforestry systems of choosing shade trees that can accommodate epiphytes. This study demonstrates the remarkable diversity of ants associated with the epiphyte community of a single tree, in addition to the distinctive association between the different species of epiphytes, their physical characteristics, and their inhabiting ant fauna.

Key words: Canopy, agroforestry, cocoa plantations, *Erythrina*, habitat structure, epiphytes, suspended soil.

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Introduction

Ecological systems are extremely complex due to the multiplicity of interactions between organisms and the environment in which they live (STORK & GASTON 2004). Some factors, such as habitat structure (BELL & al. 1991, YANOVIK & al. 2004, CAMPOS & al. 2006, YANOVIK & al. 2011, NEVES & al. 2013), are important to determine the species richness of ecological communities. Usually, traditional agricultural systems are homogeneous and simple.

However, agroforestry systems retain a naturally high structural complexity compared with agricultural systems without trees (PERFECTO & al. 1996, RICE & GREENBERG 2000, SCHROTH & al. 2004). Some tropical agroforests are known for their contribution to the maintenance of vascular epiphytes (CRUZ-ANGÓN & GREENBERG 2005, HIETZ 2005, HYLANDER & NEMOMISSA 2008), and in the Neotropics for having high densities of bromeliads, similar to native for-

ests, in particular in the canopy (HIETZ & HIETZ-STEIFERT 1995). Vascular epiphytes represent 10% of the world's flora, comprising mainly bromeliads, cacti, ferns, and orchids (GENTRY & DODSON 1987), and are mostly restricted to the canopy of tropical forests (BENZING 1995, NIEDER & al. 2001).

The canopy of tropical agroforests, just as the canopy of rainforests, has high structural complexity, which partially results from the occurrence of epiphytes in tree crowns (BENZING 1990, YANOVIK & al. 2004, HIETZ 2005, MOFFETT 2013). These epiphytes can play an extremely important role in the maintenance of the abundance and diversity of ants and other arthropods in Neotropical forest canopies (KITCHING & al. 1997, BENZING 2000, STUNTZ & al. 2003, YANOVIK & al. 2004, RODGERS & KITCHING 2011). In addition, epiphytes also contribute to the biotic complexity of agroecosystems (CRUZ-ANGÓN & GREENBERG 2005, PHILPOTT & al. 2008, CRUZ-ANGÓN & al. 2009), which demonstrates their importance as a structural element in the tropical canopy. Ants are the taxon with largest biomass among canopy invertebrates (TOBIN 1995, DAVIDSON & al. 2003). In the tropics, canopy ants represent around half the diversity of the whole Formicidae family (FLOREN & al. 2014) and are between the most active groups in the occupation of epiphytes, given their capacity to move and aggregate soil, biomass, and humus. Several authors suggest that epiphyte architecture and the suspended soil associated with epiphyte roots and bromeliad rosettes affect the fauna of invertebrates that inhabit the canopy of tropical forests (PAOLETTI & al. 1991, YANOVIK & al. 2004, RODGERS & KITCHING 2011).

However, due to sampling limitations, those systems and the interactions that occur in them are still poorly known. Several studies on the arthropod fauna that inhabits the upper canopy were based on chemical shock (canopy fogging) (ERWIN & SCOTT 1980, ERWIN 1983, DIAL & al. 2006, RICHTER & al. 2007, CRUZ-ANGÓN & al. 2009). Nevertheless, previous studies show that this technique, in spite of being frequently used in tropical environments, does not allow to sample all arboreal species in Neotropical forest canopies especially when epiphytes are a major structural component (YANOVIK & al. 2003). Consequently, the largest problem with massive invertebrate sampling is the difficulty in associating the specimens collected with a particular habitat or microhabitat. Hence, limited ecological information can be obtained from such method, for example for studying territorial ant mosaics (RIBEIRO & ESPÍRITO SANTO 2007).

Some studies have shown the importance of host plant architecture to explain the arthropod richness and composition associated with plants (e.g., BASSET & NOVOTNY 1999, CAMPOS & al. 2006). The influence of epiphytes on canopy arthropods remains unknown, in spite of some studies on the role of epiphytes in this environment (YANOVIK & al. 2004, CRUZ-ANGÓN & al. 2009, YANOVIK & al. 2011). Architecture of epiphytes, occurrence of suspended soils and epiphyte diversity are some of the variables that have been investigated to explain the structure of the canopy arthropod fauna (STUNTZ & al. 2002b, YANOVIK & al. 2004, GONÇALVES-SOUZA & al. 2011, RODGERS & KITCHING 2011, YANOVIK & al. 2011). Studies on the importance of epiphytes in the structuring of the arboreal arthropod community are still scarce in forests and agroecosystems.

In the present study, we investigated the effects of bromeliads and canopy structure on the ant community found associated with epiphytic bromeliads of a tree crown in an agroforestry system. We tested the following hypotheses: (I) the bromeliad structure and location (distance from the tree centre) in the canopy affect ant species richness; (II) epiphytes with suspended soil support higher ant species richness; (III) the composition of ant assemblages differs between bromeliads with and without suspended soil and also as a function of bromeliad size; (IV) epiphyte-dwelling ant species follow a heterogeneous distribution and respond to epiphyte genera and species differently.

Methods

Study area: The present study was carried out in March 2007, in a cocoa agroforest (14° 45.3' S, 39° 13.9' W), which belongs to the Cocoa Research Center (CEPEC / CEPLAC) at Ilhéus, in the state of Bahia, north-eastern Brazil. The annual average temperature in Ilhéus is 24.7°C, with a seasonal range of 18 - 26°C. Annual rainfall varies from 1,300 to 2,000 mm, and annual average relative humidity is 80 - 90% (MORI & BOOM 1983). The region's main biome is the Atlantic Forest and its main economical activity is cocoa plantation (DELABIE & al. 2007, CASSANO & al. 2008). The agroforestry model known as "clear-cutting" predominates in the study site. This system consists of cocoa crops shaded almost exclusively by *Erythrina* trees. The tree *Erythrina fusca* LOUR. (Fabaceae) has a Neotropical origin (KASS 1998), was introduced in the area and is currently extremely common in the cocoa-producing region of Bahia. In this region, *E. fusca* is widely used as a shade-providing tree to cocoa crops, mainly due to its perfect adaptation to the humid areas where cocoa is cultivated.

Sampling design: In the present study, we sampled all epiphytic bromeliads found in the canopy of a single individual *Erythrina fusca* tree 25 m in height. Some other epiphytes present in the crown of the host tree (phorophyte) were excluded from the analysis, mainly because they lacked a rosette structure and represented only a very small proportion of the total biomass of epiphytes in the tree. These epiphytes were small and belonged to Bryophyta, Pteridophyta and Orchidaceae (*Cataglyphis* sp.). The tree canopy was accessed by climbing using single the rope technique (PERRY 1978).

Epiphytes and associated fauna: To collect bromeliads with and without suspended soil and their associated fauna, we used a cloth collector with a 70 × 100 cm opening, 90 cm in height tied to a rectangular iron frame (Fig. 1), which is hereafter referred to as a "canopy hamper". The canopy hamper was connected to a rope that passed through a pulley fixed to the highest point of the canopy, which allowed its suspension from one of the main branches of the phorophyte, in order to be positioned immediately below the epiphyte to be collected. The system is meant to slow down the fall of the epiphyte when it is dislodged with a large chisel (160 cm long and with a blade 20 cm wide). The canopy hamper was developed to collect the epiphyte with its suspended soil and associated fauna, so that it could be studied when brought to the ground. Several structural measurements of the epiphyte were then taken and a preliminary collection was carried out in the field, in order to separate the suspended soil and the most agile animals.



Fig. 1: (A, B) Use of the canopy hamper, installed in the crown below the epiphyte to be collected; (C, D) bromeliad epiphyte collected with all the organic matter and suspended soil retained between its roots and leaves.

Ants, other invertebrates and even vertebrates were captured by hand, and then the rest of the material was placed in a Winkler trap (BESTELMEYER & al. 2000), used mainly to extract the mesofauna living in suspended soil (PAOLETTI & al. 1991, RODGERS & KITCHING 2011). The ants were sorted to species or morphospecies and the genera identified based on the method developed by BOLTON (1994); nomenclature followed BOLTON (2015). Voucher specimens were deposited in the Laboratório de Mirmecologia, Cocoa Research Centre CEPEC / CEPLAC (Ilhéus, Bahia, Brazil), and the Centre's reference collection was used in aiding identification.

Epiphyte distribution and architecture: All bromeliads of the tree crown were sampled and identified to the species or morphospecies level using the collection of the CEPEC Herbarium, Cocoa Research Center, Ilhéus, Bahia, Brazil as reference. We also determined the: (1) height of the bromeliad from the ground, determined from the bromeliad anchorage on the branch or twig, (2) distance to the central axis of the crown (hereafter referred as "DNC"),

(3) presence or absence of suspended soil, (4) length of the most internal and most external leaves of the rosette, (5) width at the base of the most external leaf of the rosette, (6) rosette diameter, measured at the point where the leaves are no longer coalescent, (7) number of leaves per rosette, and (8) circumference of the phorophyte branch at the point of anchorage of the bromeliad.

Organic matter deposits inside the bromeliad rosette and between leaves are offering a foraging, sheltering and nesting place for ants. We approximated the central part of the rosette to a cylinder whose volume V (cm³) was calculated as follows:

$$V = \pi r^2 * h$$

with r = rosette radius [half of measure "6" above] (cm) and h = length of the most internal leaf (cm).

Statistical analyses: We used a hierarchical partitioning to determine which structural variables (volume, number of leaves, length of the most internal and most external leaves, width at the base of the most external leaf), affected ant species richness. Hierarchical partitioning pro-

Tab. 1: Ant species collected associated with epiphytic bromeliads, present in the crown of *Erythrina fusca* LOUR. (Fabaceae). The occurrence of habitat (arboreal strict [cavities in twigs and bark] (a) and hypogeic [litter or suspended soil] (h)), and the number of occurrence of ant species throughout the sampling. n. i.* = unidentified genus.

Subfamily	Habitat	Suspended soil		Occurrence	Bromeliad genera			
Species		Absence	Presence		<i>Aechmea</i> (n = 4)	n. i.* (n = 16)	<i>Hohenber- gia</i> (n = 13)	<i>Vriesea</i> (n = 19)
Dolichoderinae								
<i>Azteca instabilis</i> (F. SMITH, 1862)	a	15	8	23	1	5	9	8
<i>Linepithema anathema</i> WILD, 2007	h		2	2		1	1	
<i>Linepithema humile</i> (MAYR, 1868)	h		1	1			1	
Ectatomminae								
<i>Gnamptogenys moelleri</i> FOREL, 1912	h		1	1		1		
Formicinae								
<i>Camponotus balzani</i> EMERY, 1894	a		2	2		1	1	
<i>Camponotus claviscapus</i> FOREL, 1899	a		4	4	1	1	2	
<i>Camponotus crassus</i> MAYR, 1862	a		7	7	1	1	5	
<i>Camponotus sexguttatus</i> (FABRICIUS, 1793)	a		2	2	1	1		
<i>Nylanderia fulva</i> (MAYR, 1862)	a	5	13	18	1	6	10	1
<i>Nylanderia</i> sp. 1	a		1	1			1	
Myrmicinae								
<i>Cephalotes atratus</i> (LINNAEUS, 1758)	a		4	4	1	2	1	
<i>Cephalotes goeldii</i> (FOREL, 1912)	a		2	2		1	1	
<i>Cephalotes pusillus</i> (KLUG, 1824)	a		5	5		4	1	
<i>Cephalotes umbraculatus</i> (FABRICIUS, 1804)	a	1	4	5		3	1	1
<i>Crematogaster acuta</i> (FABRICIUS, 1804)	a		8	8		6	2	
<i>Crematogaster erecta</i> MAYR, 1866	a	1	8	9	2	4	3	
<i>Crematogaster nigropilosa</i> MAYR, 1870	a		5	5	1	2	2	
<i>Cyphomyrmex transversus</i> EMERY, 1894	h		2	2			2	
<i>Eurhopalothrix</i> sp.	h	1	2	3			2	1
<i>Nesomyrmex tristani</i> (EMERY, 1896)	a	1	5	6		2	3	
<i>Pheidole asperithorax</i> EMERY, 1894	?		8	8	1	4	3	
<i>Pheidole</i> prox. <i>cardinalis</i>	?		11	11	2	7	2	
<i>Pheidole</i> gp. <i>flavens</i> sp. 2	?		4	4			4	
<i>Pheidole</i> gp. <i>flavens</i> sp. 3	?		2	2		1	1	
<i>Procryptocerus hylaeus</i> KEMPF, 1951	a		3	3	1	1	1	
<i>Procryptocerus spiniperdus</i> FOREL, 1899	a		2	2			2	
<i>Rogeria foreli</i> EMERY, 1894	h		1	1		1		
<i>Solenopsis</i> sp. 1	h	3	1	3	1	1	1	
<i>Solenopsis</i> sp. 2	h	2		2		2		
<i>Solenopsis</i> sp. 3	h	1	1	1	1			
<i>Strumigenys denticulata</i> MAYR, 1887	h	1		1			1	
<i>Strumigenys dolichognata</i> WEBER, 1934	h	1		1		1		
<i>Strumigenys elongata</i> ROGER, 1863	h	4	1	4	1	2	1	
<i>Strumigenys smithii</i> FOREL, 1886	h	1		1			1	
Ponerinae								
<i>Anochetus hohenbergiae</i> FEITOSA & DELABIE, 2012	a	1	4	5			5	
<i>Hypoponera opacior</i> (FOREL, 1893)	h		4	4		3	1	
<i>Hypoponera</i> sp.1	h		1	1			1	
<i>Neoponera inversa</i> (F. SMITH, 1858)	h	1		1		1		
<i>Neoponera moesta</i> (MAYR, 1870)	a	2	3	5		2	2	1
<i>Neoponera villosa</i> (FABRICIUS, 1804)	a	2	11	13		6	5	2
<i>Odontomachus haematodus</i> (LINNAEUS, 1758)	a / h		15	15	2	8	5	
<i>Pachycondyla harpax</i> (FABRICIUS, 1804)	h		2	2			2	
<i>Platythyrea sinuata</i> (ROGER, 1860)	a		1	1			1	

Pseudomyrmecinae								
<i>Pseudomyrmex gracilis</i> (FABRICIUS, 1804)	a	2	5	7	1	2	4	
<i>Pseudomyrmex</i> gp. <i>pallidus</i> sp. 1	a		1	1			1	
<i>Pseudomyrmex tenuis</i> (FABRICIUS, 1804)	a		2	2		1	1	
<i>Pseudomyrmex termitarius</i> (F. SMITH, 1855)	a		1	1		1		
Ant species per bromeliad genus					16	33	39	6
Ant species exclusively found on one bromeliad genus					1	5	12	0

cedures were performed with the package hier.part (CHEVAN & SUTHERLAND 1991, MAC NALLY & WALSH 2004). Then, we used a generalized linear model (GLM) (CRAWLEY 2007) to estimate the effect of these pre-selected structural variables, bromeliad locations in the crown ("DNC"), epiphyte genera and presence / absence of suspended soil (explanatory variables) on ant species richness (response variable). We conducted additional residual analyses to check data adequacy to the chosen probability distribution, as well as error distribution for all models (CRAWLEY 2007). When significant differences were observed between bromeliads, the data were submitted to contrast analysis by aggregating levels (CRAWLEY 2007). If the level of aggregation was not significant and did not alter the deviance explained by the null model, the levels were pooled together (contrast analyses).

We performed non-metric multidimensional scaling (NMDS) to address the hypotheses about variations of ant species composition according to the structure, volume, presence / absence of suspended soil, and bromeliad genera and species. Using a permutation multivariate analysis of variance (PERMANOVA, ANDERSON 2001), we tested the influence of volume, presence / absence of suspended soil, bromeliad genera, and bromeliad species on ant species composition, using the Jaccard distance and 999 permutations. PERMANOVA is a permutation ANOVA, which was developed to test the simultaneous response of one or more variables to one or more factors. PERMANOVA uses the "Adonis" procedure in the vegan package for R (OKSANEN & al. 2013). We also used NMDS to represent the results of the PERMANOVA analyses. In the NMDS, we also used the Jaccard for the ordination of species composition. All analyses were performed in the software R (R DEVELOPMENT CORE TEAM 2014).

Results

We studied a total of 52 bromeliads of the genera *Hohenbergia* SCHULT.f. (n = 13; 3 species), *Vriesea* LINDL. (n = 19; 3 species), *Aechmea* RUIZ & PAV. (n = 4; 1 species), and one unidentified bromeliad species (n. i.) (n = 16; 1 species). None of the *Vriesea* species (*Vriesea procera* MART. ex SCHULT. f., *Vriesea* sp. 1, and *Vriesea* sp. 2) aggregated suspended soil. By contrast part of the other bromeliad species (*Hohenbergia blanchetii* (E. MORREN.) (n = 5), *Hohenbergia* sp. 1 (n = 4), *Hohenbergia* sp. 2 (n = 1), *Aechmea* sp. 1 (n = 4), and Bromeliaceae (n. i.) (n = 9) aggregated suspended soil in their roots and among the rosette leaves. Ants were present in 36 (69.2%) of the 52 epiphytes sampled (Tab. 1). We found a total of 47 ant species of 21 genera and six subfamilies (Tab. 1). Ant species richness varied from zero to 14 species per bromeliad. We recorded a total of 42 ant species in bromeliads with

Tab. 2: Analyses of deviance of the minimal adequate models showing the effects of volume, location of the bromeliad in relation to the central vertical axis (DNC), genera and suspended soil (explanatory variables) on the species ant richness (response variable) in the canopy of a single *Erythrina* in an agroecosystem. The error distribution used in the model was Quasi-Poisson.

Explanatory variables	df	Deviance	P
Volume	1	50.90	< 0.001
DNC	1	11.08	0.01
Genera	1	64.06	< 0.001
Suspended soil	1	30.50	< 0.001

suspended soil (29 exclusively in this habitat) and only 18 species in bromeliads without suspended soil (5 exclusively in this habitat). Myrmicinae and Ponerinae were the most frequent subfamilies, with 24 and nine species, respectively, and represented together 70% of all species collected. 34% of the ant species sampled were typically hypogeic (Tab. 1). Only one ant species, *Anochetus hohenbergiae* FEITOSA & DELABIE, 2012, was found only in a single bromeliad genus, *Hohenbergia* spp. (Tab. 1) (FEITOSA & al. 2012).

Ant species richness was positively correlated to bromeliad size (volume) ($p < 0.001$, Tab. 2, Fig. 2a). We also observed a significant negative correlation between location of the bromeliad in the crown (DNC) and ant richness ($p = 0.01$, Tab. 2, Fig. 2b), where the ant species richness was associated to bromeliads localized nearest to the central axis of the crown.

Bromeliads taxa that presented suspended soil showed higher ant species richness than bromeliads without suspended soil ($p < 0.001$, Tab. 2, Fig. 3). The occurrence of suspended soil in bromeliads significantly increased their ant species richness ($p < 0.001$, Tab. 2, Fig. 3). The average ant species richness did not differ among *Aechmea*, unidentified bromeliad (NI), and *Hohenbergia* ($\text{Deviance}_{2,49} = -2.873$, $p > 0.05$), but was significantly lower in *Vriesea* bromeliads ($\text{Deviance}_{1,48} = 137.19$, $p < 0.001$). Regardless of genus, the presence of substrate increased the ant richness in bromeliads.

Ant species composition was influenced by bromeliad size, suspended soil presence, and bromeliad genus (Fig. 4, Tab. 3), but not by bromeliad species ($p > 0.05$, Tab. 3). These parameters determine the dissimilarity composition of ant species in different microhabitats of the same tree crown.

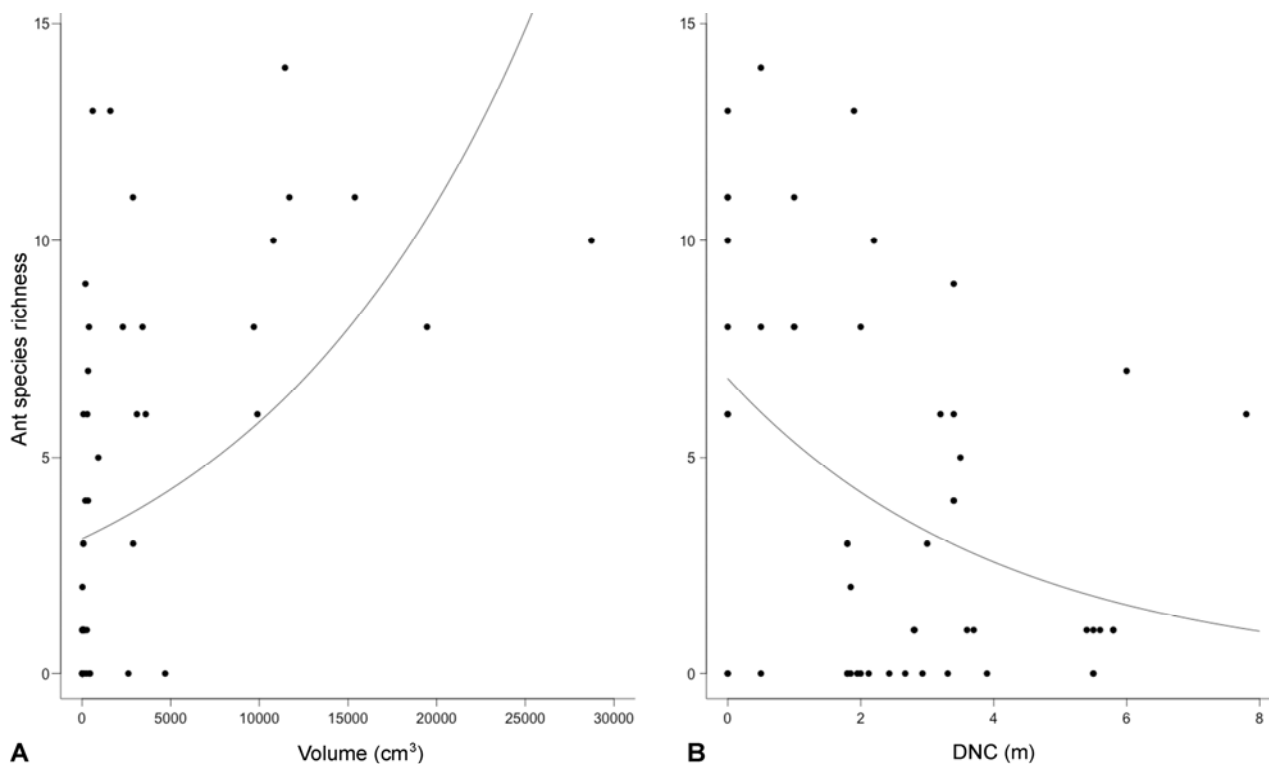


Fig. 2: Effect on ant species richness of (A) the size (volume) of bromeliads, and of (B) the distance of bromeliads to the tree central vertical axis (DNC, in m). The error distribution used in the model was Quasi-Poisson.

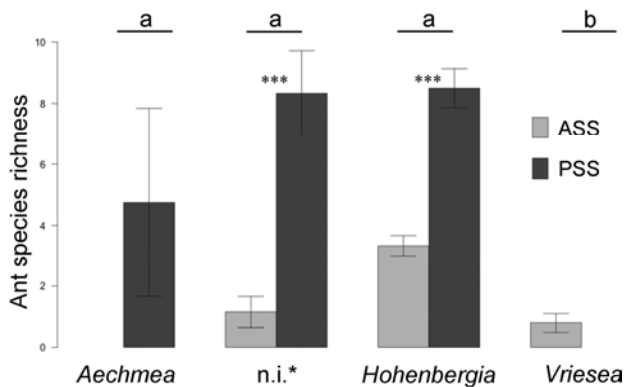


Fig. 3: Effect of the absence or presence of suspended soil on the ant species richness observed in different bromeliad genera (ASS = Absence of Suspended Soil; PSS = Presence of Suspended Soil). The vertical bars correspond to the standard error (\pm se) and (***) represent statistically different means ($P < 0.001$). Different letters above the columns represent statistically different means ($P < 0.05$). n.i.* – unidentified Bromeliaceae.

Tab. 3: PERMANOVA analysis for species composition of ants collected in 52 bromeliads present in the canopy of a single *Erythrina* in an agroecosystem.

Factors	Permanova r^2	P
Volume	0.14	< 0.001
Suspended soil	0.16	< 0.001
Bromeliad genera	0.10	< 0.003
Bromeliad species	0.05	> 0.13

Discussion

The ant species richness associated with bromeliads in the crown of a single *Erythrina fusca* tree (47 species) is the highest recorded for a single tree in a tropical agroecosystem and is comparable to the richness found in primary forests. For example, in the Peruvian Amazon, WILSON (1987) collected by insecticidal fogging 43 ant species in the canopy of a single tree. In Malaysia, YUSAH & al. (2012) found up to 45 ant species on a single tree by combining fogging, purse-string trapping, standard baiting and pitfall trapping.

We observed that bromeliad size, location (distance from the tree central axis) and presence of suspended soil influence the bromeliad ant species richness. Epiphytes may be considered as "islands" (in the island biogeography theory sense of MACARTHUR & WILSON 1967), since the number of ant species increases with the bromeliad size. This result corroborates another study on fern epiphytes (FAYLE & al. 2012), where larger ferns supported more ant colonies and species, instead of colonies with a larger population of few species, suggesting that the housing provided by the fern shelter is useful to a range of partner ants. This theory has received increasing attention in diversity studies carried out in the canopy of tropical forests, which aim at explaining the structure of ecological communities. Finally, the high ant species richness found in the present study demonstrates the importance in terms of biodiversity conservation of shade-providing trees and epiphytes (PERFECTO & al. 2003, CRUZ-ANGÓN & al. 2009, STEFFAN-DEWENTER & al. 2011, TOLEDO-ACEVES & al. 2012).

We expect that the longer the bromeliad remains on the tree, the more complex its structure becomes, as there will be favourable conditions for the deposition of organic mat-

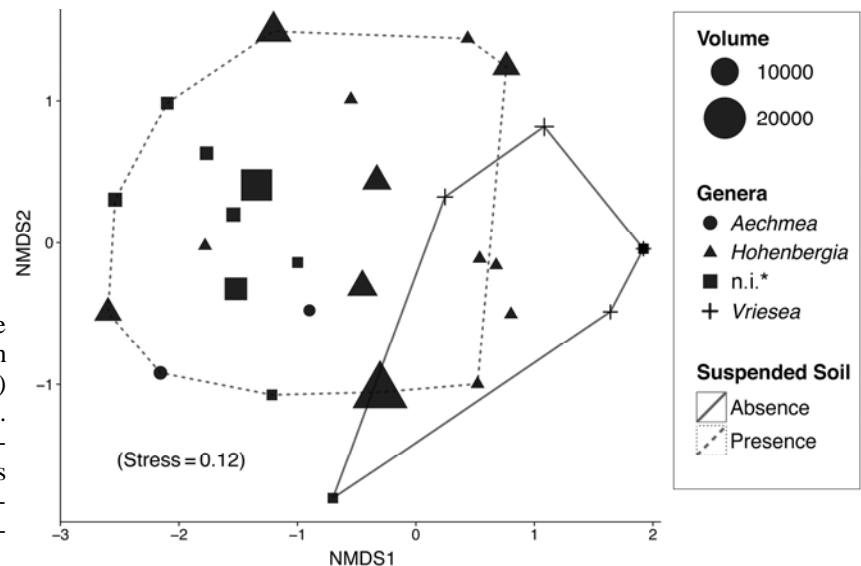


Fig. 4: NMDS analysis showing the similarity of ant species composition in bromeliads with (polygon with solid line) and without (dashed line) suspended soil. Each symbol represents a different bromeliad genus. The size of the symbols is proportional to the volume of bromeliads (cm³). n.i.* – unidentified Bromeliaceae.

ter and aggregated suspended soil, which increase the number of habitats available and provide suitable for ant nests. Resident ants may depend on epiphytes, as epiphyte size can directly affect the occurrence and structure of nesting habitats, food, and refuges (DEJEAN & al. 1995, ARMBRUSTER & al. 2002, GONÇALVES-SOUZA & al. 2011). For example, our own observations show that a large colony of *Neoponera villosa* (FABRICIUS, 1804) permanently occupied the inner cavities formed by the root entanglement of large *H. blanchetii* bromeliads, offering multiple nesting sites. A similar attractive effect for sheltering large ant colonies was observed also when groups of several small bromeliads were placed near to the trunk and branches of the phorophyte.

The location of the bromeliad also determined the richness of associated ant species. The more external to the crown, the smaller the bromeliad, and the lower was the ant richness. The tree crown architecture determines microclimatic conditions (BENZING 1995, NADKARNI & al. 2001, STUNTZ & al. 2002a, MONDRAGÓN & al. 2015) more or less favorable to colonization by the arboreal fauna. The crown edge, more exposed to wind and branch falls, is subject to broader variations of thermic amplitude and relative humidity. Other abiotic factors, such as high light incidence and low humidity, also increase from the centre of the crown, and influence the nesting and foraging area in some ant species (YANOVIK & KASPARI 2000, KERSCH & FONSECA 2005).

The presence of suspended soil is one of the main factors that determine the composition of the ant assemblage associated with bromeliads. This result corroborates other studies (PAOLETTI & al. 1991, RODGERS & KITCHING 2011) carried out in tropical forests that assessed the presence of suspended soil as a resource for invertebrates. In addition to large and abundant bromeliads (Bromeliaceae n.i. and *Hohenbergia* spp.) harbouring more ant species per rosette, the presence of the substrate alone contributes to increase ant richness.

A large size together with the presence of suspended soil can provide a larger amount and better quality of food and nesting resources for ants, and, hence, sustain higher species richness. This corroborates DEJEAN & al. (1995)

study, which suggested that there might be an influence of epiphyte size and associated cavities. According to ARMBRUSTER & al. (2002), the structural complexity of epiphytic bromeliads explains the variation in animal species found in them. When the bromeliad is larger, it retains a larger amount of water and leaf litter, and, hence, can harbour a larger amount of associated macroarthropods, as the number of microhabitats increases (FRANK 1983, ARMBRUSTER & al. 2002), larger bromeliads are presumably also older and therefore there will have been more time for ants to colonize. In the present study, ant species richness was substantially higher with *Hohenbergia*, *Aechmea* and unidentified Bromeliaceae (n.i.) than *Vriesea*.

The PERMANOVA results showed that the presence of suspended soil and the volume of the bromeliad lead not only to higher ant species richness, but also affected the composition of ant species in different microhabitats of the same tree crown. Our results corroborate those of PAOLETTI & al. (1991) and RODGERS & KITCHING (2011), who studied other invertebrate groups such as Collembola in forest canopies. RODGERS & KITCHING (2011) detected differences in the composition of the Collembola assemblage found in the suspended leaf litter of epiphytes along a vertical gradient and among seasons. This may explain differences in ant species composition found in the present study. Some terricolous ant species, such as *Pachycondyla harpax*, had their first record of canopy nesting restricted to bromeliads with suspended soil aggregated to their rosettes and roots. The same occurred with the arboreal ant *Anochetus hohenbergiae* (FEITOSA & al. 2012), with four occurrences (out of five observations) in bromeliads with suspended soil. This suggests, therefore, a specificity of some species for particular structural resources that occur in the canopy.

There were differences between bromeliad genera in terms of ant assemblage composition. The differences in ant species composition resulted clearly from differences in the fauna associated with the genus *Hohenbergia*, and were more obvious in 12 ant species, for example *Anochetus hohenbergiae* and *Pheidole* sp. *flavens* sp. 2 (Tab. 1). Preferential ant-plant relationships, in particular in *Vriesea*, could be related to the plant architecture, larger size

and occurrence of suspended soil. However, the observed dissimilarity does not imply an ecological isolation of these elements of the fauna. Still, those differences were detected in function of idiosyncrasies and distribution of low-frequency species (see Tab. 1) and, therefore, suggest the existence of a specific substitution for each epiphyte genus. This was also observed in the PERMANOVA analysis for the presence and absence of suspended soil and bromeliad volume.

The marked differences in ant species distribution among bromeliad genera suggests an effect of dominant ants (DAVIDSON 1998, DEJEAN & al. 2007) on species composition and distribution of ants on trees (LESTON 1978, MAJER & al. 1994), especially related to bromeliad distribution within the tree crown. Hence, the heterogeneous distribution of ant species among bromeliads may result from the location of bromeliads in the phorophyte's crown: either distant or close to the central axis. In other words, the tree crown is heterogeneous in terms of microclimate. Less demanding species in terms of microclimate or that better control nesting resources (dominant) spread all over the crown, whereas the less abundant species or more specialized in terms of microclimate are restricted to specific microhabitats. Hence, temporary regions, such as potential nesting sites provided by dry leaves in the periphery of the rosette, can favour the least abundant species (e.g., *Camponotus claviscapus* FOREL, 1899 and *Procryptocerus hylaeus* KEMPF, 1951). FAYLE & al. (2015) also showed that similar-sized ant species tend to exclude each other from epiphytes (bird's nest ferns).

Despite its limitations due to a lack of replication our study shows that even introduced shade species such as *Erythrina fusca* can support a large biodiversity of canopy arthropods because it provides adequate support for a large diversity of epiphytes. Epiphytes represent a key resource in forest canopies, in particular in agroforestry systems (CRUZ-ANGÓN & al. 2009, YANOVIK & al. 2011). However, the clear-cutting management regime used in the study area certainly has the great disadvantage of eliminating native tree species, which impoverishes the managed forest that has survived for many years in association with a so-called cabruca system. In the cabruca system, part of the native forest is preserved and the cocoa is planted in its understory (SCHROTH & al. 2011). Hence, to understand how the canopy can compensate for part of this biodiversity loss through epiphytes is crucial for elaborating strategies for the conservation of the arboreal fauna, especially if this implies the maintenance of an exotic species, such as *Erythrina*.

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